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FLORA OF THE MEDITERRANEAN BASIN IN THE CHILEAN *ESPINALES*: EVIDENCE OF COLONISATION

I. MARTÍN-FORÉS[1], M. A. CASADO[1*], I. CASTRO[2], C. OVALLE[3], A. DEL POZO[4], B. ACOSTA-GALLO[1], L. SÁNCHEZ-JARDÓN[1] AND J. M. DE MIGUEL[1]

[1]Departamento de Ecología. Facultad de Biología. Universidad Complutense de Madrid. Madrid (España). [2]Departamento de Ecología. Facultad de Ciencias. Universidad Autónoma de Madrid. Madrid (España). [3]Instituto de Investigaciones Agropecuarias INIA-La Cruz. La Cruz (Chile). [4]Facultad de Ciencias Agrarias. Universidad de Talca. Talca (Chile).

*Author for correspondence: M.A. Casado (macasado@bio.ucm.es).

SUMMARY

In Chile's Mediterranean region, over 18% of plant species are alien. This is particularly noteworthy in some agrosilvopastoral systems such as the *espinales*, which are functionally very similar to the Spanish *dehesas* and are of great ecological and socioeconomic interest. In the present paper we analyse Chile's non-native flora, considering three scales of analysis: national, regional (the central region, presenting a Mediterranean climate) and at community level (the *espinales* within the central region). We compare this flora with that recorded in areas of the Iberian Peninsula with similar lithological and geomorphological characteristics, and land use. We discuss possible mechanisms that might have been operating in the floristic colonisation from the Mediterranean Basin to Chile's Mediterranean region.

Key words: Alien plants, biogeography, Chile, life cycle, Spain.

INTRODUCTION

Historically, the transit of goods, domestic animals and people has favoured the flow of wild organisms around the planet (Lodge *et al*., 2006), a fact that is often associated with the introduction of cultural systems, which have contributed to generating new environmental and socioeconomic scenarios (Le Houérou, 1981; Hobbs, 1998; Grenon and Batisse, 1989). The current globalisation process is increasing landscape changes and ecosystem disruptions by human disturbance and therefore facilitating

Bases de datos: http://polired.upm.es/index.php/pastos (España), AGRIS (Italia), CAB Abstracts (Reino Unido), CABI Full Text (Reino Unido), Catálogo LATINDEX (México), DIALNET (España), ICYT Ciencia y Tecnología (España)

the transit of organisms (Paskoff and Manríquez, 1999; Rouget *et al*., 2003; Dukes and Monney, 2004; Schwartz *et al*., 2006). These 'assisted dispersals' enable species to cross biogeographical boundaries that have previously limited their distributions. Species that have been transported from one region to another are defined as alien or exotic to that newly occupied region (Richardson *et al*., 2000). Most of these species fail to establish self-perpetuating populations, but some of them do succeed and become naturalized (Sax and Brown, 2000). Regardless of the factors enabling establishment, the main consequence of this naturalisation is that alien species significantly contribute to the global floristic (taxonomic and phylogenetic) homogenization of regional floras (Winter *et al*., 2009). Despite the fact that introduction of species increases diversity at short temporal and small spatial scales, in the medium and long term, interactions with native species can lead to extinctions (Pyšek and Richardson, 2006). The net effect will depend upon the spatial and temporal scales considered and on the balance between naturalisations and extinctions (Sax *et al*., 2002). Nonetheless, the resulting ecological consequence is the coexistence of native species with exotic ones, quite often in the same community. The origin and composition of these novel communities are of great interest to understand their functioning and possible management.

Transcontinental naturalisation in Chile's flora

Mediterranean-type ecosystems around the world offer a great chance to compare and understand the mechanisms determining the success of species introduced into a given region (Kruger *et al*., 1989; Groves and Di Castri, 1991). The different regions presenting a Mediterranean climate have had different environmental histories associated with the density of human populations as well as the time and intensity of the changes that people have caused in the territory. In the Mediterranean Basin, anthropic modification of the landscape is millenary; however, rates of species extinction and naturalisation are low in comparison with other Mediterranean regions (Greuter, 1994). This fact is explained as a process of co-evolution of plants with people (Di Castri, 1981). Conversely, other Mediterranean areas have undergone a rapid change following successive cultural colonisations, some of these relatively recent, a fact that accounts for the current ecological conditions threatening the biodiversity of these areas (Underwood *et al*., 2009).

As with other Mediterranean regions, Chile is recognised as a biodiversity hotspot (Ormazabal, 1993), with high levels of regional and national endemism, possibly related with its biogeographic isolation (Myers *et al*., 2000). Its flora comprises 5364 native taxa, including species and subspecies (Marticorena and Quezada, 1985; Marticorena and Rodriguez, 1995, 2001) and between 552 and 723 alien species, depending on the

author considered (Arroyo *et al*., 2000; Castro and Jaksic, 2008). Paradoxically, despite the large amount of alien species present and their early colonisation, Chile has been considered a region that has been less invaded or is in an earlier stage of invasion than other Mediterranean regions of the world (Arroyo *et al*., 2000; Figueroa *et al*., 2004; Castro and Jaksic, 2008).

The arrival of exotic species to Chile started with the European colonisation in the XVI century (Arroyo *et al*., 2000; Figueroa *et al*., 2004), which marked the first deliberate introduction of animals and plants (Montenegro *et al*., 1991; Jaksic, 1998). The rate of species entry in these early days is unknown, since the initial systematic botanic descriptions of flora date from the XVIII century and were performed by botanists who were more interested in describing the native species than the exotic ones (Gay, 1845-1854; Reiche, 1896-1911). By the end of the XVIII century, numerous exotic species had become naturalised in Chile (Figueroa *et al*., 2004), such as *Cardamine hirsuta* L., *Medicago polymorpha* L., *Spartium junceum* L. and *Bromus hordeaceus* L. (Castro *et al*., 2005). Although this species introduction has not been consistent over time, a rate of two to three species per year is estimated, which is lower than the four to six species recorded for other Mediterranean regions (Groves, 1991; Kloot, 1991, Rejmánek *et al*., 1991; Wu *et al*., 2003).

Processes and mechanisms in species introduction

Changes in land use constitute the main factor determining processes of colonisation and naturalisation of plant species (Le Houérou, 1991; Huston, 1994; Holmgrem *et al*., 2000). Among the most influential factors, deforestation, fires and particularly agricultural practices have been highlighted (Le Houérou, 1991; Cowling *et al*., 1996; Williamson, 1996; Hobbs, 1998). With regard to deforestation, although Chile still has one of the biggest areas of temperate forest in South America (Donoso, 1993), much of it has been deforested for pastures or croplands. This process started in the XVI century, although the main boom was during the middle of the XX century, with the expansion and intensification of wheat crops (Echeverría *et al*., 2006) and the spread of forestry plantations. In relation to fire, unlike other Mediterranean climate areas, fire has not constituted a factor of natural disturbance in Chile (Muñoz and Fuentes, 1989; Gómez-González and Cavieres, 2009), a fact that accounts of the absence of specific adaptations in native species. Although there is evidence of fires of human origin in earliest settlements in the region, around 14 000 years ago, these were not significant until the arrival of the Spanish (Aronson *et al*., 1998; Aravena *et al*., 2003; Villa-Martínez *et al*., 2003). Subsequently, fires became more frequent and intense, and currently about 5000 ha of native scrubland are burnt each year, the vast majority of these fires being

intentional (Gómez-González and Cavieres, 2009). It has been suggested that plant communities under novel fire regimes are more susceptible to invasion than those under a natural (historical) fire regime (Trabaud, 1991; D'Antonio, 2000). However, different studies that have analysed the effects of fire upon native and non-native Chilean flora appear to indicate that fire is not a relevant factor with regard to favouring non-native species (Keeley and Johnson, 1977; Holmgrem *et al*. 2000; Gómez-González *et al*., 2010). Fire does, however, constitute a notable advantage for the establishment of annual plants, which are poorly represented in Chile's native flora (Arroyo *et al*., 1995).

The implementation of European agricultural culture in the XVI century leaded to big changes in land uses and landscapes in Chile, the extent of which are yet not well known (Turner *et al*., 1995). The effects of agriculture have been both direct (ploughing, cropping and grazing) and indirect (fire and deforestation, employed as techniques for preparing the land for agriculture and livestock farming). Livestock was introduced into Chile, perhaps at the same time as the colonisation by Europeans. Other herbivores, however, such as rabbits and hares, were brought more recently, in the XIX century (Jaksic and Soriger, 1981). Several studies have associated the naturalisation of exotic plant species with grazing by both livestock (Holmgren *et al*., 2000; Pauchard and Alaback, 2004; Del Pozo *et al*., 2006; HilleRisLambers *et al*., 2010) and rabbits (Sáiz and Ojeda, 1988; Holmgren *et al*., 2000; Holmgren, 2002). The effect of grazing on native or non-native species has been characterised using morphofunctional plant traits, revealing differences in their response. For instance, grazing appears to favour some exotic creeping species, such as *Erodium cicutarium* (L.) L'Hér. and some leguminous species, in detriment to the upright ones, the latter more closely associated with native species (Holmgren *et al*., 2000). Grazing also favours substitution of native hemicryptophytes by both native and non-native annuals, capable of resisting periods of drought stress as seeds.

Many exotic plants were also introduced associated with crops, and became widely distributed as a result of the importance of agriculture in the country (Castro *et al*., 2005). Crop fields, particularly along their succession stages following abandonment, constitute the ecosystems presenting the highest values for richness and cover of non-native plants in Chile (Figueroa *et al*., 2011). Since colonisation the introduction process has continued, although with different rates along time. Thus, Aronson *et al*. (1998) highlight an initial wave of exotic species from 1880 to 1920 associated with transformation of the landscape. Fuentes *et al*. (2008) recognise an initial phase (1910-1940) associated with intense development of agriculture (Cariola and Sunkel, 1982), as well as a second phase (1980-2000) related with a sharp increase in the mechanisation of farms and forest plantations at large scale. Matthei (1995) describes a sustained increase

in the naturalisation of exotic species from 1894 to 1934 associated with wheat imported from other countries.

Although many species were accidentally introduced into Chile (Arroyo *et al*., 2000), many were taken for agricultural, medicinal, culinary and, more recently, ornamental purposes. Since the arrival of the Spanish, species were introduced associated with hay for livestock fodder and with wool and cereals. Endozoochory likely constitutes the most frequent mechanism of effective seed dispersal. However, during transit from Spain to Chile, exozoochory was probably the most effective means of dispersal, given the difference in time between the transoceanic voyage and the time required for seeds to pass through an animal's digestive tract (generally less than 1 week; Malo and Suárez, 1997). Europe was not the only centre of introduction of non-native species to Chile. During the Gold Rush, in the middle of the XIX century, there was intense wheat trading with California (Davis, 1894), a fact which mobilised other species, together with grain and straw, in both directions (Le Houérou, 1991; Jiménez *et al*., 2008), especially from Chile to California.

Comparative studies of transcontinental naturalisation

Comparison of non-native floras between climatically similar regions constitutes a very useful tool for understanding aspects associated with the species naturalisation process (Pauchard *et al*., 2004, Hierro *et al*., 2005). It can help us to understand the effects of changes in the landscape associated with historical or cultural scenarios upon the naturalisation process (Kruger *et al*., 1989; Aschman, 1991). Among comparative studies of different regions with Mediterranean climates, those between Chile and California have been intensely analysed (e.g. Parsons, 1976; Arroyo *et al*., 1995; Holmgren *et al*., 2000; Pauchard *et al*., 2004; Jiménez *et al*., 2008). These researches highlight the large number of species common to both regions (386, which is 64% of Chile's non-native flora; Pauchard *et al*., 2004), as well as the fact that their communities are undergoing different process of invasion with similar consequences of floristic homogenization (Figueroa *et al*., 2011). However, to date there have been no comparative studies between Chile and Spain, despite their climatic and geomorphological similarity, the historical relationships that favoured the entry of species into Chile and the large number of species common to both countries. Many of these naturalised species are associated with the *espinal*, an agroecosystem presenting a management system and structure similar to those of the Spanish *dehesa* (Ovalle and Avendaño, 1987; Ovalle *et al*., 1990). However, as these agricultural systems are similar in both countries, we are not fully aware of the mechanisms underlying the arrival of determined species and the subsequent naturalisation and spread thereof.

The aim of this paper is to analyse the relative significance of the biogeographic origin, lifecycle and representativeness of taxonomic families in Chile's non-native flora. We considered three scales of analysis: national, regional (the central zone presenting a Mediterranean climate) and community (the *espinales* within the central zones). In the third case, we also conducted a comparative study with Mediterranean grasslands from the Iberian Peninsula in order to identify the degree of similarity in the floristic composition of communities with comparable ecological and agronomic characteristics.

MATERIAL AND METHODS

Study area

The *espinal* is an anthropic savannoid formation characterised by dispersed trees of *Acacia caven* Mol. (the *espino*) within an herbaceous matrix comprising mainly annual plants of Mediterranean origin (Olivares and Gastó, 1971; Ovalle *et al*., 2005; del Pozo *et al*., 2006). It supports a rural population of approximately 350 000 people, as well as the largest Chilean livestock: 800 000 sheep and 250 000 cows. It covers an area of two million hectares in Chile's central zone, ranging along the Central Valley and the western slopes of the Coastal mountain range (Ovalle *et al*., 1999). It currently occupies mainly the dryland sectors (Figure 1), from the river Petorca (32° S), bordering on the arid Mediterranean region, to the river Laja (37º S), bordering on the perhumid region (Fuenzalida and Pisano, 1965; Di Castri, 1968; Quintanilla, 1981; Rodríguez *et al*., 1983). Further north, in the arid and perarid regions, some *espinales* can be found, preferentially located in valley bottoms (Follman and Matte, 1963; Rodríguez *et al*., 1983). Their distribution is associated with Mediterranean-climate areas, albeit with very variable annual rainfall, from 160-200 mm at its northern limit and up to 1000-1200 mm at the southern one. It presents high species diversity (Gulmon, 1977; Solbrig *et al*., 2002; Del Pozo *et al*., 2002) and to date, 215 species have been identified only in the Cauquenes region (Ovalle *et al*., 1987). It originated through changes in land uses after the Spanish conquest; the native sclerophyllous forest was cleared in order to open up land for agriculture and livestock farming, which favoured gradual invasion by the exotic species *A. caven* (Gulmon, 1977; Armesto and Pickett, 1985; Ovalle *et al*., 1990), possibly from South America's Gran Chaco (Holmgren, 2002).

The *espinal* is an agrosilvopastoral system presenting much similarity with the Spanish *dehesas* and Portuguese *montados*. It has traditionally been based upon two models of management: continuous extensive grazing in flatlands, occasionally inundated during winter, and rotation of grazing and cereal cropping in the better drained hillsides (Ovalle *et al*., 2005). In the latter case, the *espino* is periodically cut

down for firewood and charcoal. The land is subsequently ploughed for sowing cereal crops. After one or two years' harvest, depending upon the fertility of the soil, the land is abandoned and colonised by herbaceous species, while shoots grow from the stump of the *espino*. In this phase, the land is used for extensive grazing with a low stocking rate of approximately one sheep/ha (Del Pozo *et al*., 2006). The grazing period prior to the following cropping cycle is variable, from three to 40 years, depending on the fertility of the soil.

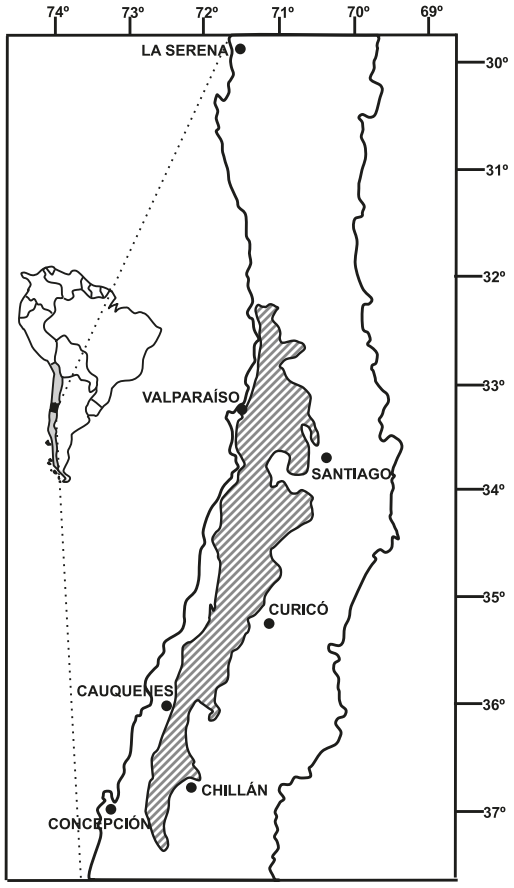


FIGURE 1

Location of Chile (in grey) in South America and enlargement of the Central zone. The shaded area represents the main distribution areas of espinal (modified from Ovalle *et al.,* 1999).

Localización de Chile (en gris) dentro de Sudamérica y ampliación de la Zona Central. La región sombreada representa el área de distribución de los espinales (modificado de Ovalle et al., 1999).

The *espinal* is currently more degraded than in past times. In the first place, an increasingly greater area of the *espinales* in the Central Valley is being replaced by intensive irrigation agriculture. Furthermore, many owners have abandoned their traditional farming activities for forest plantations (approximately 80 000 ha/year), mainly of *Pinus radiata* D. Don or *Eucalyptus globulus* Labill. Finally, the territory still maintaining functional *espinales* has usually low fertility and soil erosion, leading to low agricultural production. At present, 40% of the area is occupied by *espinales* with very little tree cover (<25%) and 4% is dominated by *romerillo* (*Baccharis linearis* (Ruiz and Pav.) Pers.), which indicates a situation of degradation and abandonment. Under these circumstances, the cereal-pasture rotation system is in decline and limited to small areas, almost exclusively for people's own consumption.

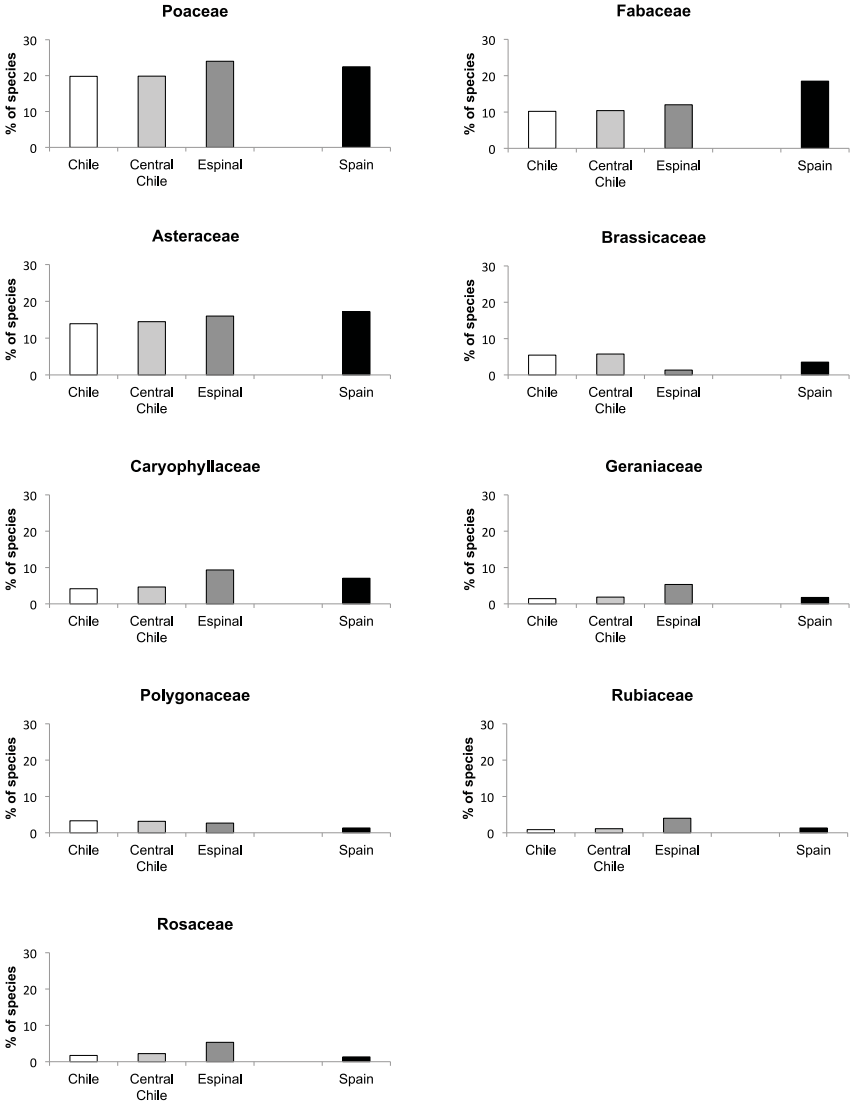
Methodology

For our research we developed a database containing all non-native species found in Chile. We used the catalogue of Chilean flora by Marticorena and Quezada (1985, 1987), along with information provided by the *Laboratorio de Invasiones Biológicas de la Universidad de Concepción* (http://www.lib.udec.cl/database.html). This list was complemented with an extensive bibliographic revision incorporating some exotic species recently cited in the country. Each species was characterised by assigning its taxonomic family, area of origin, life cycle and distribution range within Chile. To assign the area of origin and life cycle we used different regional floras, fundamentally *Flora Iberica* (Castroviejo *et al*., 1986-2010), *Flora Europaea* (Tutin *et al*., 1964-80) and *Flora del Cono Sur* (Zuloaga *et al*., 2008). As regions of origin we considered the four big continents: Eurasia, Africa, America and Australasia. Apart from these four large regions we considered independently the Mediterranean Basin (SE, S and SW of Europe, N Africa and SW Asia), given the non-native typology of species present in Chile. Species present in more than one continent were classified as Cosmopolitan. As for the life cycle trait, we classified them into three groups: annual, perennial herbaceous and woody species. Finally, for the distribution range within Chile we took the 15 administrative regions as units (from the Tarapacá Region in the far north to the Magallanes Region at the southern limit), excluding the species present only on the islands belonging to Chile (Easter Island and the Juan Fernández archipelago). We obtained these data mainly from Castro *et al*. (2005), Martincorena (http://www.lib.udec.cl/database.html) and Zuloaga *et al*. (2008). We considered the set of non-native species present throughout the country, as well as those distributed only in the central zone (from the Coquimbo region in the north to the Bío-Bío Region in the south; Figure 1).

In order to complement our database of non-native species, in 2010 we conducted field samplings, both in Chilean *espinales* and in Spanish Mediterranean grasslands. In each country we selected 15 sites and in each one we chose two 10 x 10 m plots in which we randomly distributed six 50 x 50 cm quadrants. In each quadrant we recorded the presence of all plant species. Each species was assigned a value of frequency according to the number of sites in which it was recorded in each country. The 30 sites selected presented similar lithological characteristics (acidic materials associated with igneous or metamorphic rocks), geomorphological ones (undulating topography) and those relating to use history (management for extensive livestock farming). In the case of Chile the 15 sites were distributed within the Mediterranean region, over more than 600 km, from 32º 31' 35'' to 37º 00' 10'' S latitude. In the case of Spain the 15 sites were distributed within the centre-western areas (Extremadura, N Andalucía and W Castilla-La Mancha, from 40º 14' 45'' to 37º 51' 40'' N latitude). For all species of European origin, we standardised the nomenclature in accordance with *Flora Iberica* (Castroviejo *et al*., 1986-2010), and in the case of families as yet unpublished in this study, with *Flora Europaea* (Tutin *et al*., 1964-80).

RESULTS

The list of Chile's non-native flora comprises 773 species or subspecies, which, following exclusion of spurious citations, was reduced to 698 taxa (548 in the central zone and 75 in the *espinales*), 50 of which are woody species and the rest herbaceous ones. This large set of species is distributed into 72 families, of which the best represented ones at country scale are Poaceae (19.8% of species), Asteraceae (13.9%) and Fabaceae (10.2%). This distribution of species into families is very similar when the Chile's central zone was exclusively considered (Figure 2). However, the spectrum of families present in the flora of the *espinales* is very different, and is characterised by a higher proportion of Poaceae, Caryophylaceae, Rubiaceae, Rosaceae and Geraniaceae, and a decrease in the proportion of Brassicaceae. This distribution into families of the *espinales* is relatively similar to that seen in Spanish grasslands, except for the fact that Spain presents more Fabaceae (18.5% vs 12%) and Brassicaceae (3.5% vs 1.3%), and the *espinales* more Caryophylaceae (9.3% vs 7.1%), Rubiaceae (4% vs 1.3%), Rosaceae (5.3 vs 1.3%) and Geraniaceae (5.3% vs 1.8%).



Each histogram shows the frequency calculated at country scale (white bars; n = 698 species), of Chile's central zone (light grey bars; n = 547 species) and of the espinales (dark grey bars; n = 75 species). In the case of Spanish grasslands (black bars) frequency was calculated with the total number of species found in the field samplings (n = 229 species)

FIGURE 2

Frequency histograms of the distribution of non-native species according to taxonomic families. Only the nine most represented families are shown.

Histogramas de frecuencia de la distribución de las especies no nativas según la familia a la que pertenecen. Solo se muestran las nueve familias mejor representadas.

With regard to the area of origin of Chile's non-native species, at the scale both of country and of the central zone, species of Eurasian origin (39.7%) dominate and, to a lesser degree, those of Mediterranean origin (28.4%) (Figure 3). However, when only the flora of the *espinales* is considered, the species from the Mediterranean Basin increase to 49.3% and those of Eurasian origin to 48%, thus Eurasia in the broader sense constitutes the area of origin of 97.3% of non-native species. This tendency is maintained in Spanish grasslands, with values of 97.8% for species from Eurasia (72.1 and 25.7% for species of Mediterranean and Eurasian origin, respectively).

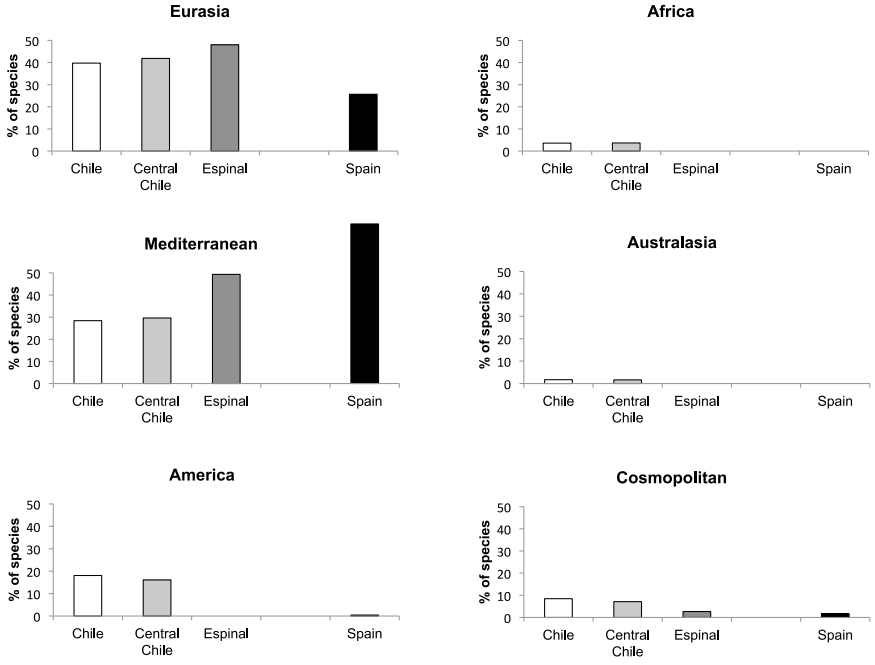


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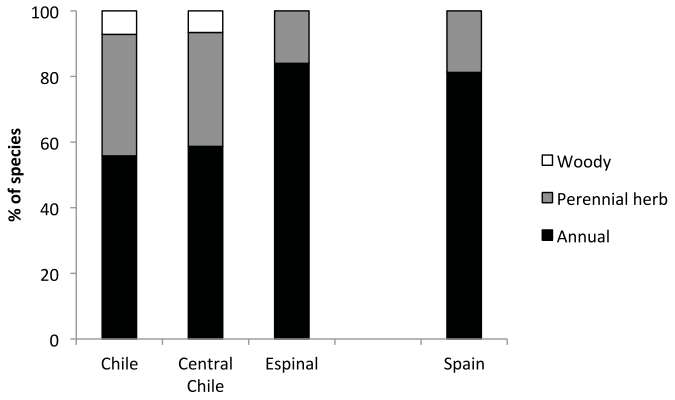
FIGURE 3

Frequency histograms of the distribution of non-native species according to region of origin.

Histogramas de frecuencia de la distribución de las especies no nativas según la región biogeográfica de origen.

Both in Chile as a whole and in the central zone, the vast majority of non-native species are herbaceous, both annual (55.8%) and perennial (37%) (Figure 4). This trend is accentuated in the *espinales*, where none exotic woody species have been found and annual plants represent 84%, a value very similar to the 81.2% of annual species found in Spanish grasslands. Life cycle (annual, herbaceous perennial and woody) is not independent from the area of origin of the non-native species (table of contingency between areas of origin x life cycle, $\chi^2 = 169.18$, $p < 0.001$): among the species of African and American origin there are significantly more woody and perennial herbaceous plants than expected at random; among those of Mediterranean origin there are significantly more annual species; and among those of Australian origin there are significantly more woody species.



For Chile, the central zone and the espinal we only considered non-native species. For Spanish grasslands, we calculated frequency with the total number of species found in the field samplings.

FIGURE 4

Frequency histograms of the distribution of non-native species according to their life cycle: annual (black bars), perennial herbaceous (grey bars) and woody (white bars) plant.

Histogramas de frecuencia de la distribución de las especies no nativas según su forma biológica: anual (barras negras), herbácea perenne (barras grises) y leñosa (barras blancas).

In the field samplings we recorded a total of 229 species in the Spanish grasslands and 152 in the Chilean *espinales*, 49% of which were non-native. Of the 10 most common species in Spain, all but one (*Agrostis pourreti* Willd) can be found in the catalogue of non-native species of Chile; moreover, they were found in the sampling in the *espinales* (Table 1). Likewise, of the 10 most common species in the *espinales*, all but one (*Soliva sessilis* Ruiz and Pav.) are non-native and have been found in sampling conducted in Spain.

TABLE 1

List of the 10 most frequent species in Spain (a) and in Chile (b). For each species taxonomic family, distribution in Spain and Chile and frequency of appearance in each country are shown.

Listado de las 10 especies más frecuentes en España (a) y Chile (b). Para cada especie se indica la familia taxonómica, su distribución española o chilena y la frecuencia de aparición en cada país.

Species	Family	Distribution	Frequency in Spain (%)	Frequency in Chile (%)
a) Spain				
Plantago lanceolata	Plantaginaceae	Both	42.2	11.4
Bromus hordeaceus	Gramineae	Both	42.8	63.6
Trifolium campestre	Leguminosae	Both	49.7	1.9
Vulpia muralis	Gramineae	Both	50.3	22.2
Hypochoeris glabra	Compositae	Both	50. 6	61. 7
Plantago coronopus	Plantaginaceae	Both	56.9	0.1
Agrostis pourretii	Gramineae	Spain	58. 9	0.0
Trifolium glomeratum	Leguminosae	Both	58. 9	23.1
Tolpis barbata	Compositae	Both	63.1	5.3
Leontodon taraxacoides subsp. longirostris	Compositae	Both	69.4	83.3
b) Chile				
Petrorhagia prolifera	Caryophyllaceae	Both	6.4	33.6
Soliva sessilis	Compositae	Chile	0.0	33. 9
Erodium cicutarium	Geraniaceae	Both	15.8	34.7
Trifolium dubium	Leguminosae	Both	8.3	35.0
Briza minor	Gramineae	Both	4.2	46. 7
Erodium botrys	Geraniaceae	Both	3.3	49.7
Hypochoeris glabra	Compositae	Both	50. 6	61. 7
Bromus hordeaceus	Gramineae	Both	42.8	63.6
Aira caryophyllea	Gramineae	Both	8.8	64.4
Leontodon taraxacoides subsp. longirostris	Compositae	Both	69.4	83.3

DISCUSSION

Arroyo *et al*. (2000) and Figueroa *et al*. (2004) consider that in continental Chile there is a total of 707 naturalised non-native species and subspecies. This value is somewhat higher than the 698 taxa considered in this paper, approximately 12% of the total flora. Despite the fact that some recent introductions have been done, a greater amount of

species have been excluded from the list due to being spurious citations. The amount of exotic species in Chile, however, is likely higher, considering the little botanical prospection conducted in certain parts of the country. Thus, during the sampling and in view of the lack of confirmation, at least 5 species had not been previously cited: *Aphanes microcarpa* (Boiss. and Reut.) Rothm., *Logfia minima* (Sm.) Dumort., *Moenchia erecta* (L.) G. Gaertn., B. Mey. and Scherb., *Trifolium cernuum* Brot. and *Vulpia ciliata* Dumort. Considering only the central Mediterranean zone, Figueroa *et al*. (2011) recognised 2395 native species and 507 non-native ones, which account for 18% of the flora in this region (Arroyo and Cavieres, 1997; Arroyo *et al*., 2000). In this case, our data contain 548 non-native species in the central zone, a difference possibly associated with the geographic definition of this zone. This non-native flora contains a large number of families, none of which show any clear dominance, although the most common ones are Poaceae, Asteraceae and Fabaceae, in accordance with the three most invasive families worldwide (Pyšek, 1998).

Most of Chile's non-native species are annual plants (56%) of Eurasian-Mediterranean origin (68%). The dominance of exotic annual species coincides with the findings of other authors for other Mediterranean-climate regions (Le Floc'h 1991; D'Antonio and Vitousek, 1992; Cowling *et al*., 1996; Figueroa *et al*., 2004; Norton *et al*., 2007). Their rapid growth and high reproduction rates, and capacity to resist unfavourable periods in the form of seeds makes them more competitive in repeatedly disturbed open spaces, such as those created by fire, ploughing or grazing (Le Floc'h, 1991; Gómez-González *et al*., 2010). As for biogeographical origin, our results show that they are preferentially from the Mediterranean Basin or, in the broader sense, Eurasia, which would coincide with the findings of several authors for Chile and other Mediterranean-climate areas (Montenegro *et al*., 1991; Arroyo *et al*., 2000; Holmgrem *et al*., 2000; Figueroa *et al*., 2004; Castro *et al*., 2005).

The annual character and Mediterranean origin predominating in non-native Chilean plants could be related to the different use history from that of the Mediterranean Basin. The pastures of the Mediterranean basin have been subjected to an intense grazing regime involving bovines and other domestic herbivores for over 6000 years of its evolutionary history (Perevolotsky and Seligman, 1998). This long history of coexistence with natural and anthropic disturbances has determined processes of co-evolution between plants and agriculture (Di Castri, 1981; Cowling *et al*., 1996; Perevolotsky and Seligman, 1998; Holmgren, 2002; Hayes and Holl, 2003; Kimball and Schiffman, 2003; Ricotta *et al*., 2009; HilleRisLambers *et al*., 2010), which have selected the plants presenting more competitive traits in a context of continuous grazing such as, for example, forms of growth, concentration of nutrients in tissues or position of growth meristems, among others (Adler *et al*., 2004; Díaz *et al*., 2007). On the contrary,

Chile's Mediterranean region underwent a drastic transformation since the colonisation only 500 years ago and its native flora might not have co-evolved with large herbivores in the last 10 000 years. This lack of adaptation to continuous grazing means that, with the introduction of livestock, native species are negatively affected, which favours the establishment of alien species (Milchunas and Lauenroth, 1993; Holmgren *et al*., 2000; Adler *et al*., 2004; Díaz *et al*., 2007).

The flora of Central Chile is a good expression of the country's as a whole with regard to percentages of the most represented families, life cycle and origin of non-native species. This central zone, representing only 20% of Chile's territory, contains 80% of all the country's exotic plants. This high concentration of naturalised plants (Matthei, 1995) can be accounted for by a conjunction of factors relating to history, environment and land uses. Chile was conquered by land from the north through the Atacama desert into the central zone. To the south of the Bío-Bío river, the territory was not colonised until just over a century ago (Aronson *et al*., 1998). Given the arid and semiarid conditions of the North, only the central zone, with its Mediterranean climate, was suitable for agriculture and for 350 years, the species introduced were therefore relegated to this region (Fuentes *et al*., 2008). It was only as from the XX century that non-native species were introduced into the whole country, with mass and intense deforestation of the austral temperate forest (Donoso and Lara, 1996). In short, it is the central zone that has undergone the biggest change as a result of intensive agriculture for over five centuries (Montenegro *et al*., 1991; Matthei, 1995). Moreover, it is the most densely populated region (78% of the country's population, with an average of 75 inhabitants/km^2; Pauchard *et al*., 2006; INE, 2007) and with the densest roads network (Arroyo *et al*., 2000).

The representation of the non-native flora tends to be greater at more detailed spatial scales (Gaertner *et al*., 2009), a fact that can be seen in the *espinales* studied. On one hand, the percentage of non-native species therein is much higher than the 13% for the whole country or the 18% for the central zone, reaching 49%. This value is higher than the 36.8% reported by Figueroa *et al*. (2011) for *espinales* and very similar to that reported by Montenegro *et al*. (1991). At family level, the percentages of Caryophyllaceae, Rosaceae, Geraniaceae and Rubiaceae double and even quadruple the values characteristic of the country or of the central zone. On the other hand, among non-native species, annual plants show an increase from 56% for the whole country to 84%; exotic woody species were absent from our study. Finally, compared with the 68% of species of Eurasian or Mediterranean origin in Chile, the *espinales* account for 97%. In this context it is interesting to highlight the relationship between regions of origin and species' biological cycle, with a positive association among annual plants for species from the Mediterranean Basin and among woody plants for those of Australian, African

or American origin. This relationship is possibly associated with the way in which the species were introduced into the country and with the climatic characteristics of the recipient habitat: unintentionally in the case of most of the plants associated with agriculture and livestock farming (Mediterranean annual plants adapted to grazing; Holmgren, 2002) or for ornamental or forestry purposes (woody plants generally of extra-European origin; Pyšek *et al*., 2011). The extreme values found in the *espinales* (compared with the rest of Chile) referring to distribution of families, biogeographic origin and life cycle are, however, of the same order of magnitude as those found in Spanish grasslands (although proportionally Rubiaceae, Rosaceae and Geraniaceae present higher percentages in Chilean *espinales* and Brassicaceae in Spanish grasslands). Given that Europe, and specifically the Mediterranean Basin, have constituted the main source of immigration since America was discovered (Di Castri, 1991; Figueroa *et al*., 2004; Jiménez *et al*., 2008) the floristic similarity between both countries appears to indicate that the *espinales* represent a copy of Europe's agricultural model, in which not only animal and plant species (livestock, cereals and associated weeds) were introduced from Europe, but also technology (ploughing, harrowing, animal traction) and the culture associated with management of the system (fallow, rotation). The final result is an agroecosystem, the Chilean *espinal*, which not only presents great physiognomic and functional similarity with the Spanish *dehesa* (Ovalle and Avendaño, 1987; Ovalle *et al*., 1990), but is also similar with regard to the floristic characteristics evaluated in this research. There are, however, differences between these two agroecosystems, particularly with regard to species richness (much higher in Spain). It is known that the number of alien species becoming established in a given country is lower than the amount that might potentially arrive (Malo and Suárez, 1997) and the number of exotic species capable of reaching Chile is estimated at between 7 070 and 35 400 (Castro *et al*., 2005). An example is the Santiago Botanic Garden which, in the middle of the XIX century, cultivated over 2000 exotic species, 43 of which became naturalised (Matthei, 1995; Castro *et al*., 2005). These data place in doubt whether the flora of the *espinales* constitutes an impoverished version of Spanish grasslands because specific filters existed that limited the number of species arriving or, on the contrary, whether there is a predominance of the biotic and abiotic filters acting in the assemblage of communities in the *espinales*.

The entry of alien species and the extinction of native ones in a region have been considered a process of global biological homogenisation (McKinney and Lockwood, 2001; Olden, 2006; Olden and Rooney, 2006; Winter *et al*., 2009). Castro and Jaksic (2008) conclude that this homogenisation process is not yet significant in Chile, given that from colonisation times up to the present, only two species have become extinct (*Plazia cheiranthifolia* (Remy) Wedd. and *Menodora linoides* Phil.) and that the floristic similarity among regions has not significantly changed. Our data, however, and those

provided by Jiménez *et al*. (2008) and Figueroa *et al*. (2011), would seem to suggest that at least the *espinales* are being subjected to an intense homogenisation process, as can be seen in the dominance of certain species (and families) common to Spanish grasslands on the list of most frequent species in the *espinales*. The most frequent species is *Leontodon taraxacoides* (Vill.) Mérat, first recorded in Chile in 1963 (Castro *et al*., 2005), which contradicts the hypothesis that the exotic species appearing subsequent to 1950 present a narrower range within the country (Arroyo *et al*., 2000; Pauchard *et al*., 2004; Castro *et al*., 2005). This would appear to indicate that this homogenisation process has become accentuated in the last few decades.

At present the speed of change of many ecological, economic and social parameters is reaching heretofore unknown rates, and the predictions are even more drastic in reference to changes in land uses at global scale (Lugo and González, 2010; USDA, 2006). In this context of global change, there is a pressing need to understand these processes of species colonisation and naturalisation. The exchange of species, successful establishment of some of them or extinction of others undoubtedly contributes to the appearance of new environmental scenarios, with socioeconomic repercussions that are difficult to evaluate in the short term (Rockstrom *et al*., 2009). Identifying changes in ecosystem structure and functioning in the short, medium and long term constitutes a fundamental objective with regard to evaluating the "health" of ecosystems, as is stated in the objectives of the Millennium Ecosystem Assessment Programme (Millennium Ecosystem Assessment, 2005; Carpenter *et al*., 2009).

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FLORA DE LA CUENCA MEDITERRÁNEA EN LOS ESPINALES CHILENOS: EVIDENCIAS DE UNA COLONIZACIÓN

RESUMEN

En la región mediterránea de Chile más del 18% de las especies de plantas son exóticas. Este hecho es especialmente importante en algunos sistemas agrosilvopastorales, como los espinales, muy similares funcionalmente a las dehesas españolas y de gran interés ecológico y socioeconómico. En este trabajo se analiza la flora no nativa de Chile considerando tres escalas de análisis: nacional, regional (zona central de clima mediterráneo) y a escala de comunidad (los espinales dentro de la región central), comparándola con la flora registrada en áreas equivalentes de la Península Ibérica. Se discuten los posibles mecanismos que han podido operar en la colonización florística desde la cuenca mediterránea hacia la región mediterránea chilena.

Palabras clave: Biogeografía, Chile, ciclo biológico, España, especies exóticas.